Zebra mussel induced mortality of unionids in firm substrata of western Lake Erie and a habitat for survival

Don W. Schloesser[1], R. D. Smithee[2], G. D. Longton[2], and W. P. Kovalak[2]

[1]U.]S. Geological Service, Biological Resources Division, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan 48105 U. S. A.
[2]Environmental Assessment, Detroit Edison Company, 6100 W. Warren, Detroit, Michigan 48226 U. S. A.

Abstract: The present study was conducted to determine impacts of zebra mussel [*Dreissena polymorpha* (Pallas, 1771); Dreissenidae] infestation on unionids in firm substrata in western Lake Erie. Unionid mollusks were collected at a total of 15 stations on three offshore depth contours (2, 3, and 4 m) in 1983 (before zebra mussel infestation), in 1990 and 1993 (after zebra mussel infestation), and at one station on a nearshore 2-m depth contour and along one transect on a nearshore 1-m depth contour in 1993. Numbers of living unionids on substrata along offshore contours remained similar between 1983 and 1990 and then decreased from 97 individuals in 1990 to only five individuals in 1993. In addition, the number of species decreased from nine to four between 1990 and 1993. In contrast, on nearshore contours 85 living individuals representing nine species were found in 1993. About 48% of the living and 79% of the dead unionids at the two nearshore locations were covered with byssal threads of dreissenid mussels, but were not actively infested by mussels. The presence of living unionids on nearshore contours of western Lake Erie in 1993 indicates that survival of unionids in the presence of abundant zebra mussel populations can be possible in firm substrata and that these habitats can provide natural "refugia" for unionid populations. At present, we do not know what allows unionids to survive in the presence of zebra mussel colonization, but believe that water-level fluctuations and waves could contribute to the removal of mussels from unionids. This information could be of major concern in the mitigation of impacts of infestation on unionids in waters throughout North America.

Key words: *Dreissena*, Unionidae, refugia, Great Lakes, unionid mortality

Zebra mussels [*Dreissena polymorpha* (Pallas, 1771); Dreissenidae] have been shown to be ectoparasites causing reduced fitness, shell deformities, and mortality of unionids (Bivalvia: Unionidae) in waters of Europe and North America (Ricciardi *et al.*, 1995; Schloesser *et al.*, 1996). In the Laurentian Great Lakes, infestation of unionids by zebra mussels was one of the first and most visible ecological impacts of the early invasion of mussels into North America (Hebert *et al.*, 1989, 1991; Mackie, 1991; Schloesser and Kovalak, 1991; Hunter and Bailey, 1992; Haag *et al.*, 1993; Nalepa and Schloesser, 1993). Unionid mortality increased as a result of infestation and unionid populations were nearly eliminated in some areas (Gillis and Mackie, 1994; Schloesser and Nalepa, 1994; Nalepa *et al.*, 1996). In addition, zebra mussels have invaded and are believed to be causing unionid mortality in major rivers of North America, such as the Detroit, St. Lawrence, Mississippi, Ohio, and Tennessee Rivers (Tucker, 1994; Ricciardi *et al.*, 1996; Strayer and Smith, 1996; reviewed by Schloesser *et al.*, 1996).

In western Lake Erie, increased mortality of unionids attributed to zebra mussel infestation has only been documented in soft-mud substrata of open waters (> 6 m deep) (Schloesser and Nalepa, 1994). Soft substrata are believed to suffocate unionids that cannot maintain themselves at the substrate-water interface due to the added weight of infesting zebra mussels (Schloesser and Nalepa, 1994). However, unionid mortality caused by infestation has occurred in some firm-substratum habitats (*e. g.* sand and gravel) where suffocation caused by sediments is unlikely (Nalepa, 1994; Tucker, 1994; Schloesser *et al.*, 1996), but observations indicate that unionids do survive in the presence of zebra mussels on some firm substrata (DWS: unpub. data; D. Blodgett, Illinois Natural History Survey, Havana, Illinois, pers. comm.).

The present study was performed to determine changes in the unionid population in firm compacted sand substrata along the perimeter of western Lake Erie in 1983, before zebra mussels were present, and 1991 and 1993, after mussels were present. We hypothesized that if smothering in soft substrata is the only mechanism causing unionid mortality in western Lake Erie, then unionids should survive infestation in firm substrata along the perimeter of western Lake Erie.

METHODS

Unionid bivalve mollusks and infesting zebra mussels were collected at 15 stations located on three offshore depth contours (2, 3, and 4 m depths) along the perimeter of western Lake Erie between 23 August and 15 October 1983, 31 October and 11 November 1990, and 8 September and 27 October 1993 (Fig. 1). Unionids were also collected at one station on a nearshore 2-m depth contour, 9 September 1993 and in a transect area on a nearshore 1-m depth contour, 21 October 1993. The offshore 2-m and nearshore 2-m depth contours were separated by a deeper 3-m contour. Fluctuations of daily water levels were corrected based on the frame of reference of low water data at Father Point, Quebec (Great Lakes Basin Commission, 1975). In general, sampling depths were about 1 m deeper than low water datum, except for the period of time when the nearshore transect was sampled during a seiche. All living and dead unionids (represented by both valves) were collected and used in the present study. In addition, total counts of valves and shell pieces of unionids were determined in 1990 and 1993.

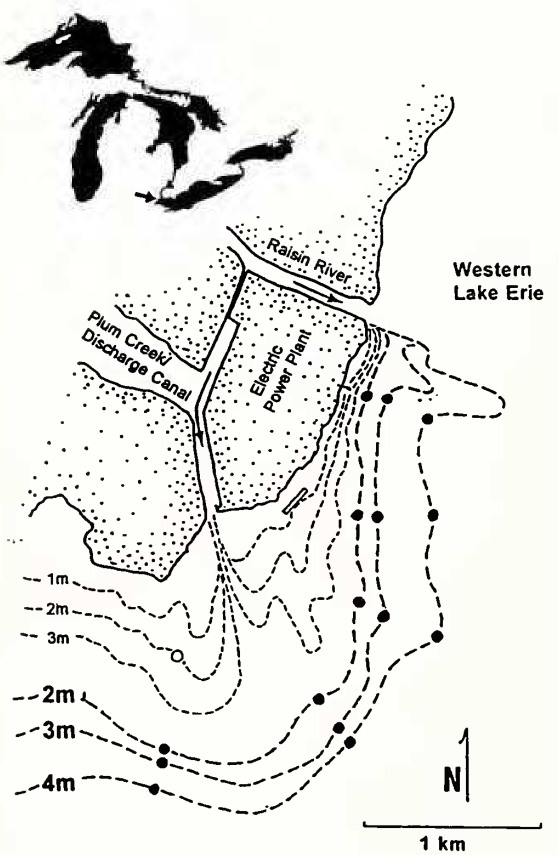

Fig. 1. Locations in western Lake Erie where unionid mollusks were sampled: at 15 stations (●) on three offshore depth contours (dark dashed lines; 2-, 3-, and 4-m) in 1983, 1990, and 1993, and at one station (○) on a nearshore 2-m depth contour (light-dashed line) and along one transect (▭) on the nearshore 1-m depth contour (light-dashed line) in 1993.

Unionids at stations on offshore contours and the nearshore 2-m depth contour were collected by SCUBA (Fig. 1). At each station, random searching was conducted for 30 min within a 50-m diameter circle. Unionids were removed from the water, individually separated, and taken to the laboratory.

Unionids in the transect area (7 m by 150 m) along the nearshore 1-m depth contour were collected by walking and manually removing exposed specimens (Fig. 1). This was possible because water in western Lake Erie was pushed away from shore by westerly winds causing a seiche, thereby dewatering substrata on the nearshore 1-m depth contour for a period of about 6 hr.

In the laboratory, up to ten randomly selected unionids and attached zebra mussels from one station on the offshore 4-m depth contour, the station on the nearshore 2-m depth contour, and the transect on the nearshore 1-m depth contour were analyzed. Living infested unionids were selected, except from the offshore, 4-m depth contour in 1993 when only dead unionids were present. Schloesser and Nalepa (1994) have shown that length-frequency distributions of zebra mussels from living and dead unionids in western Lake Erie are similar. Infesting zebra mussels were removed from individual host unionids and retained in a U. S. Standard Number 60 sieve (0.25-mm mesh). Length-frequency distributions of infesting zebra mussels were constructed from shell-length measurements in 1-m size classes. All mussels or a randomly selected sub-sample of 200-300 mussels (< 6-mm long per unionid) and all mussels > 7-mm long were measured in each sampling period. All mussels were identified and counted. All mussels were zebra mussels (*Dreissena polymorpha*); no quagga mussels (*Dreissena bugensis* Andrusov, 1897) were present in western Lake Erie (Mills *et al.*, 1993; MacIsaac, 1994). Length-frequency distributions of unmeasured mussels < 6-mm long were based on the proportions of measured sub-sampled mussels in each whole millimeter size group. This procedure has been shown to adequately determine length-frequency distributions of zebra mussels in western Lake Erie (Schloesser and Kovalak, 1991; Schloesser and Nalepa, 1994). Dry weights (in g at 105°C for 48 hr) of individual unionids and infesting mussels (a measure of infestation intensity; Schloesser and Kovalak, 1991) were determined.

Unionids were identified following Clarke (1981) and by comparison with bivalve taxonomic reference collections (Detroit Edison Company, Detroit, Michigan, and Great Lakes Science Center, Ann Arbor, Michigan). Taxonomic nomenclature follows Williams *et al.* (1993) with the exception that *Lampsilis radiata radiata* (Gmelin, 1791) was combined with *L. siliquoidea* because these two species are believed to interbreed in the Great Lakes

(Clarke, 1981). Mean numbers of living and dead unionids per station at 15 stations on the three offshore depth contours were tested by Student's t-test after $\log_{(10)} + 1$ transformation (Snedecor and Cockran, 1967).

RESULTS

UNIONIDS ON OFFSHORE CONTOURS

Numbers of living and dead unionids changed substantially on the three offshore depth contours in western Lake Erie between 1983 and 1993 (Table 1). In 1983, total mean number of living unionids per station was significantly greater (paired t-tests, $P \leq 0.05$) than dead unionids. In 1990 and 1993, total mean numbers of dead unionids were significantly higher than living unionids. Numbers of living unionids remained about the same between 1983 and 1990: 85 and 97 individuals, respectively. Then they decreased significantly from 97 in 1990 to only five in 1993. Numbers of dead unionids increased significantly from nine in 1983 to 360 in 1990, then decreased to 157 in 1993. In 1983, mean numbers of living individuals were significantly greater than numbers of dead individuals on the 2-m and 4-m depth contours; in 1990, there were significantly more numbers of dead than living individuals on the 3-m and 4-m depth contours. In 1993, the numbers of dead individuals was greater than the number of living on all contours. Between 1983 and 1990, the number of living unionids increased on the 2-m and 3-m depth contours and decreased on the 4-m depth contour. The greatest increase in the number of dead unionids occurred on the 4-m depth contour between 1983 and 1990.

Numbers of living unionid species decreased on offshore depth contours in western Lake Erie between 1983 and 1993 (Table 2). Twelve living species were found in 1983, nine species in 1990, and four species in 1993. Between 1983 and 1990, the number of species on the 2-m and 3-m depth contours increased from seven to nine, whereas the number on the 4-m depth contour decreased from 12 to six species. In 1993, only four species (*Amblema plicata plicata, Lampsilis siliquoidea, Potamilus alatus,* and *Quadrula quadrula*) represented by five individuals were found on the 2-m and 3-m depth contours.

Table 1. Numbers of living and dead unionids collected at 15 stations on three offshore depth contours in western Lake Erie, 1983, 1990, and 1993. (*; significant difference [$P \leq 0.05$] in mean number of unionids per station).

Depth (m)	1983 Living		1983 Dead	1990 Living		1990 Dead	1993 Living		1993 Dead
2	19	*	1	31		26	2		20
3	12		3	27	*	59	3		41
4	54	*	5	39	*	[1]275	0	*	96
Total	85	*	9	97	*	360	5	*	157

[1]significant (P = 0.060).

UNIONIDS ON NEARSHORE CONTOURS

Relatively large numbers of living unionids occurred in sampled areas on the nearshore 2-m and 1-m depth contours (Table 3). A total of 85 living unionids represented by nine species occurred at nearshore locations. Only living unionids (55 individuals, represented by eight species) were collected at the nearshore 2-m depth station. Both living (30 individuals, represented by five species) and dead (29 individuals, represented by ten species) unionids were found in the transect area on the nearshore 1-m depth contour.

Only 15% (17 of 114 individuals) of the unionid shells collected on nearshore contours were infested with zebra mussels (Table 3). In addition, 70% (80 of 114) only showed evidence of past infestation (*i. e.* only byssal threads present on unionid shells). Evidence of infestation was absent on 15% (17) of individual shells (10% [11] of these were living and 5% [6] were dead unionids).

INFESTING ZEBRA MUSSELS

Mean dry weights of infesting zebra mussels were substantially higher on the offshore 4-m depth contour than on the nearshore 2-m depth contour; no infestation occurred on the 1-m nearshore depth contour (Table 4). On the offshore contour in 1990, mean infestation weights on living and dead unionids were 41.1 and 36.3 g/unionid, respectively; in 1993, infestation weights decreased to 32.9 and 27.6 g/unionid, respectively. In general, weights of infesting zebra mussels were about equal to host unionid weights on the offshore contour. In nearshore areas, weights of infesting zebra mussels ranged between 0.5 and 4.4 g/unionid, and mean infestation weights were substantially less than mean unionid weights.

Length-frequency distributions of zebra mussels removed from unionids collected on the offshore 4-m depth contour and the nearshore 2-m depth contour in Fall 1993 were substantially different (Fig. 2). Mussels on the offshore contour were larger (mean = 12 mm long) than those on the nearshore contour (mean = 6 mm long). Peak distribution of mussels on unionids from the offshore contour was between 12 and 16 mm, whereas the peak distribution of mussels on the nearshore contour was between 3 and 7 mm.

DISCUSSION

UNIONID MORTALITY ON OFFSHORE CONTOURS

The present study, that by Nalepa (1994) in Lake St. Clair immediately upstream of western Lake Erie, observations by Tucker (1994) in the Mississippi River, and data of

Table 2. Numbers of living unionids collected at 15 stations on three offshore depth contours in western Lake Erie, 1983, 1990, and 1993. (–, none collected).

Species	1983 Depth (m)			1990 Depth (m)			1993 Depth (m)		
	2	3	4	2	3	4	2	3	4
Amblema plicata plicata (Say, 1817)	1	1	2	12	3	12	–	2	–
Elliptio dilata (Rafinesque, 1820)	–	–	1	–	–	–	–	–	–
Fusconaia flava (Rafinesque, 1820)	2	1	16	1	2	8	–	–	–
Lampsilis ovata (Say, 1817)	–	–	2	–	1	–	–	–	–
L. siliquoidea (Barnes, 1823)	6	6	14	7	16	9	1	–	–
Leptodea fragilis (Rafinesque, 1820)	1	2	1	3	1	1	–	–	–
Ligumia recta (Lamarck, 1819)	–	–	1	–	–	–	–	–	–
Obliquaria reflexa (Rafinesque, 1820)	1	–	1	2	–	1	–	–	–
Potamilus alatus (Say, 1817)	–	–	2	–	–	–	1	–	–
Pyganodon grandis (Say, 1829)	–	–	6	–	1	–	–	–	–
Quadrula pustulosa pustulosa (Lea, 1831)	6	1	7	5	1	8	–	–	–
Q. quadrula (Rafinesque, 1820)	2	1	1	1	2	–	–	1	–
Total Species	7	6	12	7	8	6	2	2	0

Schloesser (unpub. data) indicate that high unionid mortality can occur on firm substrata where smothering by soft substrata is unlikely. In addition, recent data indicate that high unionid mortality could be occurring in areas where infestation does not exist, but zebra mussels are found on surrounding substrata (Ricciardi *et al.*, 1996; Strayer and Smith, 1996).

In the present study, zebra mussel infestation caused substantial unionid mortality (94%) in firm-sand substrata located on offshore contours of western Lake Erie between 1983 and 1993. Mortality occurred between 1990 and 1993 after five years (1989-1993) of zebra mussel colonization of nearshore waters; not between 1983 and 1990 (after one year of zebra mussel colonization) when densities of unionids actually increased. In the fall of 1989, zebra mussels became very abundant in western Lake Erie reaching densities in excess of 340,000/m^2 in open waters (> 6 m depth) and 700,000/m^2 in nearshore waters (2-3 m depth) and infestation intensities in excess of 10,000/unionid (Schloesser and Kovalak, 1991; Kovalak *et al.*, 1993;

Table 3. Numbers of living and dead unionid species with attached zebra mussels and with attached byssal threads of zebra mussels collected at one station on a nearshore 2-m depth contour, 8 September 1993, and in one transect area on a nearshore 1-m depth contour, 21 October 1993, in western Lake Erie.

	Station on Nearshore 2-m Depth Contour[1]			Transect on Nearshore 1-m Depth Contour[2]			
	Living Unionids			Living Unionids		Dead Unionids	
	Attached Zebra Mussels	Byssal Threads		Byssal Threads		Byssal Threads	
		Present	Absent	Present	Absent	Present	Absent
Amblema plicata plicata (Say, 1817)	13	12	2	13	3	8	–
Fusconaia flava (Rafinesque, 1820)	1	2	–	2	2	1	1
Lampsilis ovata (Say, 1817)	–	–	–	–	–	1	–
L. siliquoidea (Barnes, 1823)	–	1	–	1	–	2	2
Leptodea fragilis (Rafinesque, 1820)	–	1	–	–	–	2	–
Obliquaria reflexa (Rafinesque, 1820)	–	1	–	–	–	1	–
Pleurobema cordatum (Rafinesque, 1820)	–	1	1	–	–	–	–
Potamilus alatus (Say, 1817)	1	7	–	–	–	3	1
Pyganodon grandis (Say, 1829)	–	–	–	–	–	2	2
Quadrula pustulosa pustulosa (Lea, 1831)	2	7	1	3	1	2	–
Q. quadrula (Rafinesque, 1820)	–	3	–	4	1	1	–
Total Number	17	34	4	23	7	23	6
Total Species	4	8	3	5	4	10	4

[1]No dead unionids.
[2]No attached zebra mussels.

Leach, 1993; Schloesser and Nalepa, 1994). To date, mortality of unionids induced by abundant densities of zebra mussels has been documented in Europe in the mid-1930s, waters of the Great Lakes, the Hudson River and, possibly, the Mississippi River in the early-1990s (Sebestyen, 1938; Gillis and Mackie, 1994; Schloesser and Nalepa, 1994; Tucker, 1994; Nalepa *et al.*, 1996; reviewed by Schloesser *et al.*, 1996; Ricciardi *et al.*, 1996; Strayer and Smith, 1996; DWS, unpub. data).

Changes in the number of dead unionids in the study area are partly attributable to the movement of dead shells into and out of the study area. The large increase in the number of dead unionids (nine to 360) between 1983 and 1990 suggests that dead unionid shells were entering the sampled area from other areas of western Lake Erie prior to 1990. Schloesser and Nalepa (1994) have shown that at one station in open waters (> 6m deep) of western Lake Erie, mortality of infested unionids increased between Fall 1989 and Spring 1990, and by Fall 1990 was 100%. This period of time corresponds with the large increase in the number of dead unionids in the study area, especially on the offshore, 4-m depth contour in Fall 1990. In 1990, most shells appeared fresh-dead; some contained decaying tissues, many exhibited pearly nacre, and few were decalcified. In 1993, however, few shells appeared fresh-dead; no decaying tissues were found, few exhibited a pearly nacre, and most were decalcified and difficult to identify. Loss of pearly nacre is believed to occur within 6-12 mo after death (Schloesser and Nalepa, 1994; D. Neves, National Biological Service, Blacksburg, Virginia, pers. comm.). In addition, less than 5% of the valves (n = 252) collected in 1990 were described as pieces, whereas about 25% of the valves (n = 256) collected in 1993 were described as pieces. The decrease in the number of dead unionids between 1990 and 1993 is attributed to transport of shells out of the study area into shallow bays of the lake. Substrata in shallow water bays near the sampling area were largely covered with shells of dead unionids in 1993 and 1994 (DWS, GDL, RS, pers. obs.). Several of these areas (50 m by 1000 m transects) were described as "union-

Table 4. Mean (± S.E. per unionid) and range of dry weights (g) of infesting zebra mussels and, in parentheses, mean (± S.E.) and range of dry weights of unionids at stations on offshore and nearshore depth contours in western Lake Erie 1990 and 1993.

Location/Date	Living Unionids	Dead Unionids
Offshore 4-m depth contour		
1 November 1990[1]	n = 10[2]	n = 10
	41.1 ± 2.9	36.3 ± 4.9
	29.7 - 61.2	17.3 - 67.3
	(50.5 ± 9.2)	(46.1 ± 3.1)
	(21.8 - 119.9)	(29.0 - 62.1)
8 September 1993	n = 5[3]	n = 10
	32.9 ± 7.6	27.6 ± 2.8
	6.8 - 49.0	15.1 - 40.3
	(39.8 ± 18.0)	(73.3 ± 10.5)
	(32.8 - 118.1)	(27.5 - 123.0)
Nearshore 2-m depth contour		
9 September 1993	n = 10	n = 0
	4.4 ± 2.0	
	0.5 - 19.0	
	(106.9 ± 12.4)	
	(61.7 - 188.0)	
Nearshore 1-m depth contour		
21 October 1993	n = 30	n = 29
	0	0
	0	0
	(85.7 ± 8.0)	(79.8 ± 7.2)
	(28.4 - 158.5)	(24.4 - 164.6)

[1]Most southwestern station (Fig. 1, open circle) on offshore, 4-m depth contour.

[2]Number of unionids.

[3]Offshore 2-m and 3-m depth contour; no living unionids along the offshore 4-m depth contour.

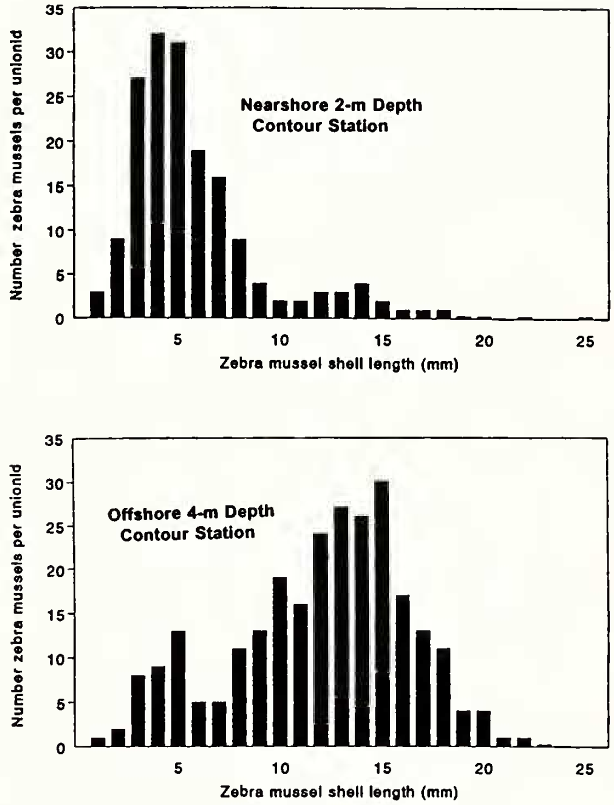

Fig. 2 . Length-frequency distributions of zebra mussels infesting unionid mollusks collected on the nearshore 2-m depth contour and the most western station on the offshore 4-m depth contour in western Lake Erie, 8 September 1993.

id graveyards" with a paved-like bottom of unionid shells. Large accumulations of dead unionids has rarely been seen in the Great Lakes prior to colonization by zebra mussels (Neves, 1987; WPK, Michigan, pers. obs.).

Survival of a few unionids on offshore contours in western Lake Erie supports the data of Schloesser and Nalepa (1994) and Nalepa *et al.* (1996) that infestation on unionids by zebra mussels does not cause 100% mortality of all unionids, but does reduce the population to < 5% of pre-zebra mussel colonization. The survival of a few unionids along the offshore 2-m and 3-m depth contours (five living of 157 total unionids) in 1993 is similar to that (four living of 191 total unionids) found in open waters of western Lake Erie in 1991 (Schloesser and Nalepa, 1994). However, the long-term viability of unionid populations at low densities has been questioned, even in the absence of infestation (Lefevre and Curtis, 1910; Downing and Downing, 1992; Downing *et al.*, 1993). To date, artificial maintenance of infested unionids has shown that survival of individual unionids in waters of western Lake Erie is possible (Schloesser, 1996).

Mean weights of zebra mussels infesting unionids on offshore contours (27.6-41.1 g/unionid) were similar to weights of infesting mussels that have caused nearly 100% mortality of unionids in other studies in western Lake Erie (Schloesser and Kovalak, 1991; Schloesser and Nalepa, 1994; GDL and RS, pers. obs.). In 1989, immediately after zebra mussels increased exponentially in western Lake Erie, weights of infesting mussels were between 30.0 and 54.9 g/unionid in nearshore waters and between 9.0 and 75.3 g/unionid in open waters (Schloesser and Kovalak, 1991; Schloesser and Nalepa, 1994). In 1990, weights in open waters ranged from 2.3 to 40.8 g/unionid (Schloesser and Nalepa, 1994). These data indicate that weights of infestation that equal or exceed host unionid weights cause severe mortality of unionids in western Lake Erie (similarly noted as mean:mass ratios by Ricciardi *et al.*, 1996).

UNIONID SURVIVAL IN NEARSHORE WATERS

Relatively large numbers of living infested unionids and living unionids showing evidence of past infestation on nearshore-depth contours indicates that zebra mussel induced mortality of unionids could be minimal or does not exist in some areas along the perimeter of western Lake Erie. The high incidence of infestation (90%) of living unionids on nearshore contours indicates that infestation did occur and that mortality of unionids could have occurred. However, temporal variation in the number of mussels per unionid and densities of mussels colonizing adjacent bottom substrata were not assessed in the present study, and these factors are believed to influence zebra mussel induced mortality of unionids (Schloesser and Kovalak, 1991; Ricciardi *et al.*, 1995; Schloesser *et al.*, 1996).

At present, the reason unionids survive in the nearshore area of western Lake Erie is not known. Several studies have suggested that some species of unionids are more likely to survive zebra mussel infestation than other species (Haag *et al.*, 1993; Nalepa, 1994; Gillis and Mackie, 1994; Tucker, 1994). Possible explanations for these observations include; unionid sex (males less impacted), robustness of shells (unionid species with robust shells less impacted), and length of brooding time (unionid species with short brooding periods less impacted) (reviewed by Schloesser *et al.*, 1996). In the present study, robust species with short brooding times (*Amblema plicata plicata, Fusconaia flava, Quadrula pustulosa pustulosa, Q. quadrula*) accounted for about one-half (57%) the individuals on offshore contours in 1990. By 1993, nearly all unionid individuals were extirpated from offshore contours and of those individuals remaining, three of five were robust, short-term brooder species. However, robust species with short brooding times (four above and *Pleurobema cordatum*) accounted for 87% of living unionids on nearshore contours in 1993. These data support the belief that robust shelled, short-term brooders appear to survive longer than thin-shelled, long-term brooders. But, to date, a total of 31 species of unionids have been infested by zebra mussels in North America, and none appear to be immune to impacts (reviewed by Schloesser *et al.*, 1996).

Possible explanations for survival of unionids in shallow waters of western Lake Erie is that infesting zebra mussels could be removed from unionids and surrounding substrata by predators such as fish and ducks, or mussels could release from substrata in response to unfavorable habitat conditions (Stanczykowska, 1977; French and Bur, 1993; Mitchell and Carlson, 1993; Stanczykowska and Lewandowski, 1993; Hazlett, 1994).

Length-frequency distributions of zebra mussels infesting unionids and SCUBA observations from offshore and nearshore areas indicate that removal of mussels in the nearshore area by predators is not the likely cause for low infestation of unionids in the nearshore area. Length-frequency distributions indicate that mostly small, young mussels were present on unionids in the nearshore area, whereas mostly larger, older mussels were present in the offshore area. This indicates that mussels probably leave unionids between their first and second year of life because peak modes often correspond to year-classes of mussels (Morton, 1969; Stanczykowska, 1977; Schloesser and Kovalak, 1991) and typically, length-frequency distributions of zebra mussels in Fall in western Lake Erie are bimodal (Griffiths *et al.*, 1991; Schloesser and Kovalak, 1991; Schloesser and Nalepa, 1994). In addition, similar observation by SCUBA indicate that zebra mussels attached to substrata in the nearshore area were of low density and small size compared to mussels in the offshore area (GDL and RS, pers. obs.). Because mussels have been shown to have great adhesive strength and predators tend to remove smaller mussels rather than larger mussels (Ackerman *et al.*, 1993; Eckroat *et al.*, 1993; French and Bur, 1993; Hamilton *et al.*, 1994), we believe that mussels were not removed by predators in the nearshore area. Rather, zebra mussels voluntarily released from unionids, perhaps because of factors such as waves, water-level fluctuations, and ice scour in nearshore areas (< 2-m depth). In Lake Erie, mortality of unionids has occurred in another nearshore area (2-3 m depth) where no waves, exposure due to water-level fluctuations, or ice scour occur (Schloesser and Kovalak, 1991; Schloesser 1996; WPK, unpub. data). Movement *en masse* of zebra mussels has been observed and attributed to fall storms, wave action, and ice scour in Europe and western Lake Erie (Ehrenberg, 1957; Lewandowski, 1976; Griffiths *et al.*, 1991; Nalepa and Schloesser, 1993). In the Illinois River, Tucker and Atwood (1995) suggested that changing water levels (among other factors) could have contributed to substantial decreases in numbers of zebra mussels in an area.

Areas where unionids survive in the presence of zebra mussel colonization appear to be natural "refugia" where long-term survival of unionids could be possible. Although long-term studies have not been completed, several sites have been found where unionids continue to live in the presence of zebra mussel colonization and large year-to-year fluctuations in the density of mussels in surrounding areas (Tucker and Atwood, 1995; Schloesser *et al.*, 1996; DWS, unpub. data; D. Blodgett, Illinois Natural History Survey, Havana, Illinois, and D. Miller, U. S. Army Corps of Engineers, Vicksburg, Mississippi, pers. comm.). Observations such as these lead Clarke, (1992), Masteller *et al.*, (1993), Tucker and Atwood (1995), and Schloesser (1996 and unpub. data) to identify possible refugia and/or suggest the need for the establishment of managed refugia to save unionid populations. These refugia would only be needed in a few areas where unique unionid species and populations are found because many waters in North America are unlikely to be heavily colonized by zebra mussels (Strayer, 1991). Indeed, dreissenid mussels in rivers appear to be a threat to unionids immediately below impoundments and lakes that provide mussel veligers contributing to infestation (Schloesser *et al.*, unpub. data; DWS and D. Hunter, Oakland University, Rochester, Michigan, unpub. data).

CONCLUSIONS

Results of the present study, conducted in firm-substratum areas along the perimeter of western Lake Erie, were similar to those of Schloesser and Nalepa (1994) who studied soft-substratum areas in open waters of western Lake Erie and found infestation of unionids by zebra mussels can equal 100% unionid mortality at individual sites, but not 100% mortality of unionids throughout the study area. However, the presence of living unionids in two nearshore areas in the present study indicate that natural "refugia" could exist in beach/littoral areas of western Lake Erie.

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